

Journal Pre-proof

3,500 years BP: The last survival of the mammal megafauna in the Americas

Fábio Henrique Cortes Faria, Ismar de Souza Carvalho, Hermínio Ismael de Araújo-Júnior, Celso Lira Ximenes, Edna Maria Facincani



PII: S0895-9811(25)00029-X

DOI: <https://doi.org/10.1016/j.jsames.2025.105367>

Reference: SAMES 105367

To appear in: *Journal of South American Earth Sciences*

Received Date: 5 December 2024

Revised Date: 16 January 2025

Accepted Date: 16 January 2025

Please cite this article as: Cortes Faria, F.H., de Souza Carvalho, I., Ismael de Araújo-Júnior, H., Ximenes, C.L., Facincani, E.M., 3,500 years BP: The last survival of the mammal megafauna in the Americas, *Journal of South American Earth Sciences*, <https://doi.org/10.1016/j.jsames.2025.105367>.

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

© 2025 Published by Elsevier Ltd.

3,500 years BP: The last survival of the mammal megafauna in the Americas

Fábio Henrique Cortes Faria^a, Ismar de Souza Carvalho^{a,b}, Hermínio Ismael de Araújo-Júnior^c, Celso Lira Ximenes^d, Edna Maria Facincani^e

email: fabiocortes22@gmail.com

^a Universidade Federal do Rio de Janeiro; Departamento de Geologia, Instituto de Geociências, Av. Athos da Silveira Ramos, 274, 21941-916, Rio de Janeiro, RJ, Brazil.

^b Universidade de Coimbra, Centro de Geociências, Rua Sílvio Lima, 3030-790, Coimbra, Portugal.

^c Universidade do Estado do Rio de Janeiro, Faculdade de Geologia, Departamento de Paleontologia e Estratigrafia, Rua São Francisco Xavier, 524, 20550-900, Rio de Janeiro, RJ, Brazil.

^d Museu de Pré-História de Itapipoca (MUPHI), Rua Tenente José Vicente, 887, 62500-000, Coqueiro, Itapipoca, CE, Brazil.

^e Universidade Federal do Mato Grosso do Sul, Faculdade de Engenharias, Arquitetura, Urbanismo e Geografia, Rua UFMS, 79070-900, Cidade Universitária, Campo Grande, Mato Grosso do Sul, Brazil.

Abstract: The last ages of appearance of mammalian megafauna in Brazil are associated with the Pleistocene/Holocene transition, establishing a consensus of extinction of this magnificent fauna during this period of time. In recent decades, direct dating of skeletal remains of this extinct fauna in Argentina, the Caribbean and Alaska, demonstrates that extinctions mammalian megafauna until the middle Holocene. Here, eight fragments of megafauna teeth from the Brazilian Intertropical Region were dated, in the locations of Itapipoca (Ceará State) and the Rio Miranda valley (Mato Grosso do Sul State), with the respective ages: Itapipoca – *Eremotherium laurillardi* (PDR-01: age= 6,161 ± 364 RC years BP; PDR-02: age= 7,415 ± 167 RC years BP), *Smilodon populator* (PDR-03: age= 7,803 ± 179 RC years BP), *Toxodon platensis* (PDR-05: age= 7,804 ± 226 RC years BP), *Xenorhinotherium bahiense* (PDR-06: age= 3,587 ± 112 RC years BP), *Notiomastodon platensis* (PDR-07: age= 7,940 ± 502 RC years BP) and *Palaeolama major* (PDR-09: age= 3,492 ± 165 RC years BP); Miranda river - *Eremotherium laurillardi* (PDR-11: age= 5,942 ± 294 RC years BP). The ages obtained demonstrate that the latest ages of megafauna appearance in Brazil are associated with the middle and late Holocene. In South America, the extinction of megafauna has been attributed to many causes, climate/environmental changes or even the synergy between these hypotheses. The ages obtained in this analysis, together with archaeological evidence, demonstrate that the Overkill and Blitzkrieg theories are not plausible explanations for the extinction of South American megafauna. We believe that the extinction of megafauna in South America is the result of the synergy between environmental/climatic changes between the Last Glacial Maximum and the Holocene Climatic Optimum, with selective hunting of females and young individuals, autoecological factors of megafauna as supporting agents.

Keywords: Megafauna, Geochronology, Holocene, Quaternary.

1. Introduction

The temporal distribution of Quaternary megafauna in South America is a subject of constant debate, with geochronological studies of this fauna being few in relation to the various paleontological sites recorded. The vast majority of published works present taxonomic data (e.g.; Ficarelli et al., 1995; Dudley, 1996; Cartelle, 1999; Lucas, 2009; Porpino et al., 2009, 2014; Cozzuol et al., 2012; Fernicola and Porpino, 2012; Mothé et al., 2012), demonstrating how diverse this fauna was in South America. Many previous geochronological studies have failed to obtain ages beyond the early Holocene, with the youngest ages relating to the Pleistocene/Holocene transition (e.g.; McNeish et al., 1970; Borrero, 1997; Peyre et al., 1998; Auler et al., 2006; Oliveira et al., 2010; Dantas et al., 2013; Hubbe et al., 2013; França et al., 2014), supporting the proposal for the extinction of megafauna mammals in this period. However, some studies have obtained early and middle Holocene ages (Collantes et al., 1993; Neves and Piló, 2003; Guthrie, 2004; Johnson et al., 2012; Prado et al., 2015), demonstrating that this interpretation is currently questionable.

There are several paleontological sites containing fossils of late Quaternary megafauna in the American continent, from Alaska to Patagonia. In South America, three zoogeographical regions stand out in the quantity and diversity of species of this mammal fauna, which are: Brazilian Intertropical Region (BIR; Figure 1; Pansani et al., 2016), Pampean and Chaco (Cione et al., 2009). In recent decades, there has been an effort by the Brazilian scientific community to acquire geochronological data for the Quaternary megafauna of the Brazilian Intertropical Region (BIR), most of which are from the Pleistocene/Holocene (e.g. Auler et al., 2006; Hubbe et al., 2007; Ribeiro et al., 2013; Dantas et al., 2013; França et al., 2014; Scherer et al., 2017; Faria et al., 2020a).

The Pampean region in Argentina presents distinct localities with paleontological and archaeological sites with the presence of Quaternary megafauna with Early and Middle Holocene ages (Collantes et al., 1993; Borrero, 1997; Politis and Gutiérrez, 1998; Suárez, 2003; Politis et al., 2004; Prado et al., 2005, 2015; Hubbe et al., 2007; Steele and Politis, 2009; Johnson et al., 2012). Middle and Late Holocene ages have also been recorded in Alaska (Guthrie, 2004), Cuba (MacPhee et al., 1999), and Haiti (Iturralde-Vinent et al., 2000; Steadman, 2005). Despite the growing number of geochronological studies in Brazil, paleontological sites of South American megafauna have received little attention, making it difficult to establish their temporal distribution with greater precision. Therefore, it is difficult to clarify the probable causes of megafauna extinction in South America, being the continent with the most significant loss of megafauna genera and species. (Barnosky and Lindsey, 2010).

Many studies have proposed different hypotheses for the extinction of South American mammal megafauna. Cartelle (1999) points out that the extinction of Brazilian megafauna occurred at the end of the Pleistocene, due to the cold and dry environmental conditions of the last glacial period. Ficarelli et al. (2003), based on data from Ecuador, suggest that increased aridity followed by high humidity and specific geographic factors during the Pleistocene-Holocene transition were the main conditions for this extinction event. Vivo and Carmignoto (2004) proposed that the increase in forest areas in response to increased humidity in the Mid-Holocene caused the extinction of megafauna adapted to open environments.

Steadman et al. (2005), through dating and compilation of geochronological data from the Americas, concluded that this event was asynchronous between islands and continents, favored by the activity of human hunters. Cione et al. (2003, 2009) proposed that the extinction of

mammalian megafauna in South America is a synergistic phenomenon between environmental and climatic fluctuations, autoecological factors and, also, the strong impact of anthropogenic activities (Broken Zig Zag hypothesis). Barnosky and Lindsey (2010) also pointed out to the synergy between anthropogenic activities and environmental/climatic changes, indicating that anthropogenic impacts combined with rapid climate changes during the Pleistocene/Holocene transition were the driving force for this extinction event.

This profusion of hypotheses used to explain the extinction of mammalian megafauna in the late Quaternary of South America, combined with the geochronological data available in the literature regarding the large number of paleontological sites with megafauna remains, clearly indicates the lack of consensus on the causes of the extinction event. The aim of this study is to present eight new ages for the Holocene megafauna of the BIR: from material collected at Jirau tank deposit Itapipoca, Ceará State, Brazil; and fluvial deposits from the Miranda valley (Miranda, Mato Grosso do Sul State, Brazil). As a corollary, we evaluate some proposed models of megafauna extinction in the continent.

2. Material and methods

2.1 Material

The eight dated samples are from paleontological sites in peripheral locations in the Brazilian Intertropical Region (BIR; Figure 1). Seven samples of fossil teeth (two *Eremotherium laurillardi*, dentine; one of *Smilodon populator*, enamel and dentine; one of *Notiomastodon platensis*, enamel and dentine; one of Toxodontidae indet., enamel and dentine; one of *Xenorhinotherium bahiense*, enamel and dentine; and one of *Palaeolama major*, enamel and dentine) come from the Jirau Paleontological Site (03°21'23.1" S 39°42'20.2" W; Itapipoca, Ceará State). This presents a complex taphonomic history, revealing attritional accumulation under environmental conditions with strong seasonal climate control (for more information see Araújo-Júnior et al., 2013, 2017; and Faria et al., 2020b). These fossils were provided by the Itapipoca Prehistory Museum (MUPHI), corresponding to small uncatalogued fragments from the technical reserve. A tooth fragment (dentine) taken from a mandibular branch of *Eremotherium laurillardi* (ZUFMSFOS00097) belonging to the Zoology collection of the Biology Department of the Federal University of Mato Grosso do Sul, was also dated, originating from fluvial sediments of the Miranda River (20°14'27.30"S; 56°23'59.30"W; Miranda, Mato Grosso do Sul State). These samples were selected to carry out geochronological analyzes (AMS¹⁴C) at the Radiocarbon Analysis Laboratory of the Fluminense Federal University (LAC-UFF), Brazil.

2.2 Analytical methods

2.2.1 Collagen extraction

The dentine used for dating was separated from the enamel fraction at LAC-UFF (Radiocarbon Analysis Laboratory of the Fluminense Federal University) were manually separated and observed under the microscope to identify diagenetic changes. This procedure was performed on fragments of teeth from the species *Notiomastodon platensis*, Toxodontidae, *Smilodon populator*, *Palaeolama major* and *Xenorhinotherium bahiense*, because the teeth of these taxa are composed of enamel and dentine, and dentine tissue that has collagen in its composition is used for collagen extraction. The eight samples of teeth were observed under a microscope to identify diagenetic changes and, subsequently, subsampled for chemical treatment. This was carried out in two stages, involving acid/base/acid treatment. The first, decalcification, was the addition of 3 mL of hydrochloric acid (0.5M HCl) for 36 hours, followed

by treatment with sodium hydroxide (0.1M NaOH, 30 minutes) to remove humic acids from the burial environment (Brock et al., 2010). In the second step, hydrochloric acid (0.5N HCl, 15 minutes) was added again. These steps were performed at room temperature. After that, gelatinization was performed by adding 0.01M HCL (pH 3 solution) at 65°C for 24 hours (Oliveira et al., 2021). After gelatinization, the samples proceeded to the ultrafiltration step.

2.2.2 Ultrafiltration

Collagen extraction was performed using two filters: a Millex 0.45 μm , to remove insoluble contaminants. Then, the samples were transferred to VIVASPIN 30KD ultrafilter, and centrifuged at 3,000 rpm in 10-minute cycles until 0.5 – 1.0 mL of the remaining solution (Oliveira et al., 2021). The solution was stored with the same amount of ultrapure water in the freezer for 48 hours before yarnization (Brock et al., 2010).

2.2.3 Graphitization and measurement

In order to transform the carbon into CO_2 , the material was burned at 900°C during three hours in vacuum ampoules containing cupric oxide and silver. The sample was purified in a vacuum system and transferred to a graphitization tube. The conversion of carbon dioxide into graphite takes place in vacuum-sealed ampoules containing titanium hydride, zinc and, iron in a muffle furnace at 550°C (Macario et al., 2017). The graphite was analyzed in an accelerator with a single acceleration stage, a 250 kV SSAMS from NEC, at the Instituto de Física da Universidade Federal Fluminense (Brazil), and the carbon isotope ratios were determined. Results were normalized to National Bureau of Standards oxalic acid (SEM 4990c). To verify the quality of the collagen used in the dating, analyzes of the atomic C/N ratio were carried out in the Radioecology and Environmental Change Laboratory at the Fluminense Federal University (LARA-UFF).

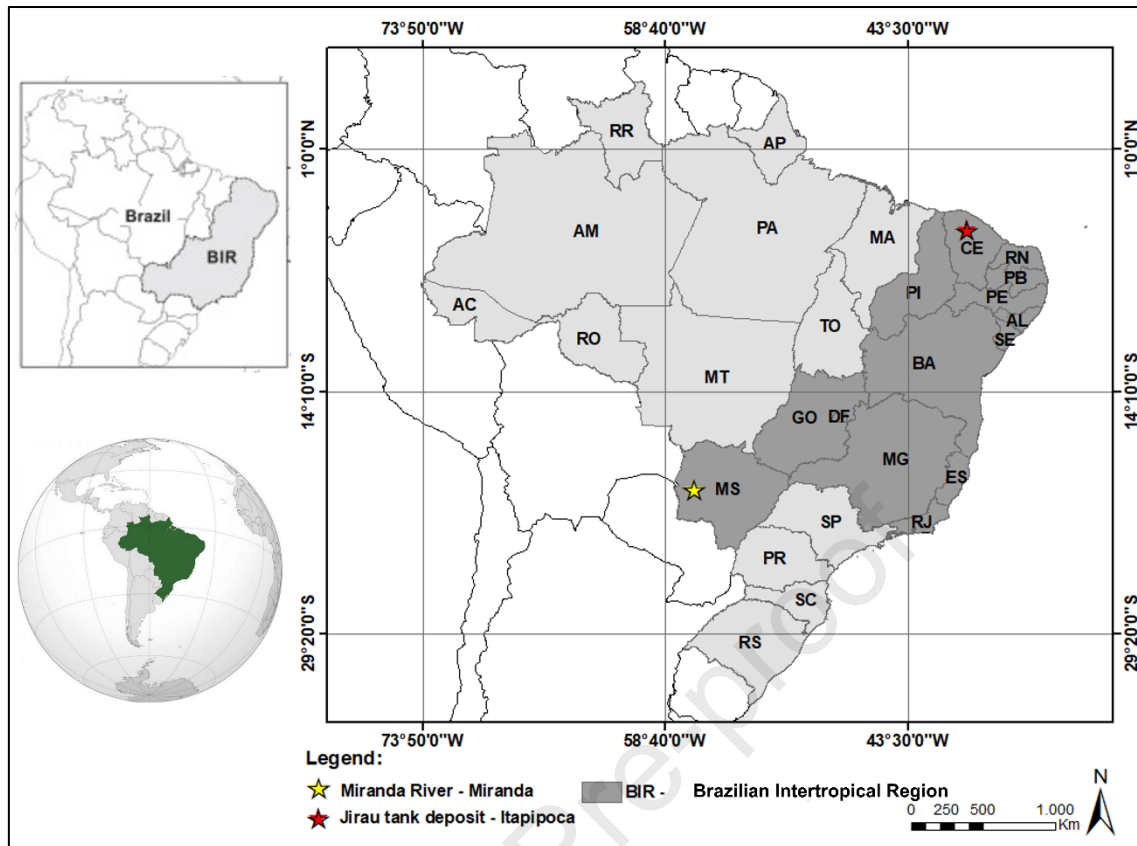


Figure 1: Location map of the Brazilian Intertropical Region in South America, showing the location of Itapipoca (Ceará State) and Miranda River (Mato Grosso do Sul State). Adapted from Pansani et al. (2019). The acronyms: BIR – Brazilian Intertropical Region; PI – Piauí State; CE – Ceará State; PB – Paraíba State; PE – Pernambuco State; RN – Rio Grande do Norte State; AL – Alagoas State; SE –Sergipe State; BA – Bahia State; GO – Goiás State; MT – Mato Grosso State; MS – Mato Grosso do Sul State; MG – Minas Gerais State; ES – Espírito Santo State; RJ – Rio de Janeiro State; SP – São Paulo State; PR – Paraná State; MA – Maranhão State; MT – Mato Grosso State; AM – Amazonas State; TO – Tocantins State; RO – Rodônia State; PA – Pará State; AP – Amapá State; RR – Roraima State; RS – Rio Grande do Sul State; AC – Acre State

3. Results

The dates obtained by AMS ^{14}C for the eight samples of megafauna fossil teeth are shown in Table 1. All ages obtained are distributed between the Middle and Late Holocene, with the youngest going well beyond the Pleistocene-Holocene boundary. Figure 2 presents the conventional radiocarbon age calibration graphs for statistical refinement, using the High Probability Density (HPD) band method for the eight dated samples. All samples were calibrated at a 95.4% confidence interval that is represented by gray areas in the graphs. Table 1 shows the respective radiometric ages and also the atomic C/N ratio of the analyzed samples.

Table 1: Radiometric ages (AMS¹⁴C) for the megafauna of Jirau and Miranda River. The acronyms: BP – before present; cal. – calibrated; (d) dentine; SD – stadard deiation; CI – confidence interval; C/N – cabon nitrogen atomic ratio. Samples PDR-01, PDR-02, PDR-03, PDR-05, PDR-06, PDR-07 and PDR-09 are samples of uncatalogued tooth fragments from the MUPHI collection of Itapipoca, Ceara State. Sample PDR-11, from the Miranda River basin, Mato Grosso do Sul State, registry number ZUFMSFOS00097 of the UFMS Zoology Collection.

Sample	Taxon	Radiocarbon date, RC yr $\pm$ 1 SD)	Calibrated age range (cal. BP; 95.4% C.I.)	C/N
PDR-01 ^(d)	<i>Eremotherium laurillardi</i>	6,161 $\pm$ 364	6,208 – 7,714	2.9
PDR-02 ^(d)	<i>Eremotherium laurillardi</i>	7,415 $\pm$ 167	7,867 – 8,536	3.1
PDR-03 ^(d)	<i>Smilodon populator</i>	7,803 $\pm$ 179	8,189 – 9,079	3
PDR-05 ^(d)	Toxodontidae indet.	7,804 $\pm$ 226	8,049 – 9,270	3
PDR-06 ^(d)	<i>Xenorhinotherium bahiense</i>	3,587 $\pm$ 112	3,493 – 4,217	3.4
PDR-07 ^(d)	<i>Notiomastodon platensis</i>	7,940 $\pm$ 502	7,836 – 10,159	2.9
PDR-09 ^(d)	<i>Palaeolama major</i>	3,492 $\pm$ 165	3,353 – 4,231	3
PDR-11 ^(d)	<i>Eremotherium laurillardi</i>	5,942 $\pm$ 294	6,120 – 7,427	3.2

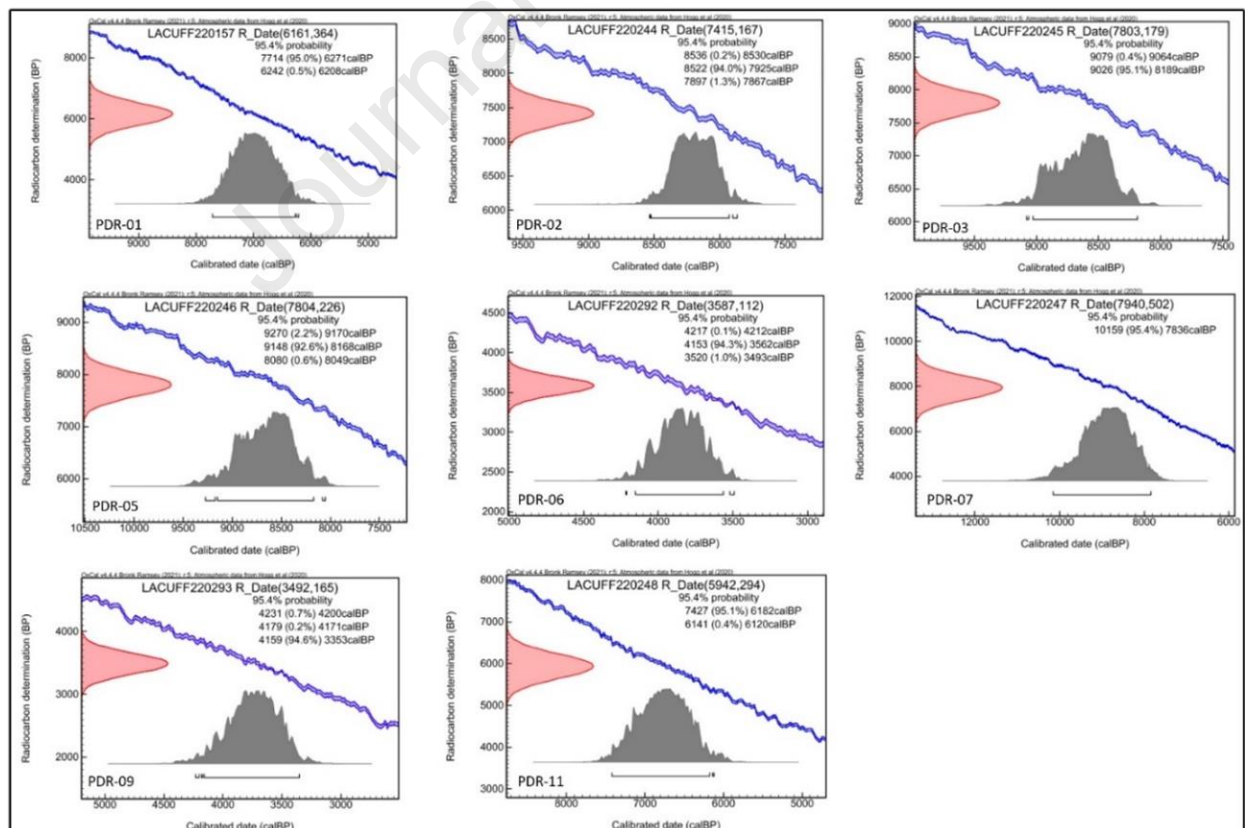


Figure 2: OxCal Calibration graphs for eight samples, obtained using the high probability density band method (HDP - High Probability Density).

4. Discussion

4.1 Collagen quality

To ensure that the collagen analyzed was not altered or degraded by diagenetic processes, we performed analyses of the C/N ratio, values between 2.9 and 3.6 are indicators of collagen preservation (DeNiro, 1985; Ambrose 1990; Bocherens et al., 2016), corroborating the results obtained.

4.2 Geochronology

The time scale for the Quaternary of South America was established in the Pampean region (Argentina), with four South American Land Mammal Ages (SALMAs): Ensenadan, Bonaerian, Lujanian and Platan (Cione and Tonni, 1999). The megafauna of BIR and Pampas are generally associated with the Bonaerian and Lujanian stages, with temporal distribution between 400,000 and 10,000 years BP (Dantas and Cozzuol, 2016). Geochronological data acquired through different methods (ESR-Electron Spin Resonance, AMS¹⁴C, ¹⁴C and U-series), indicated the presence of megafauna in the BIR between 400,000 and 9,000 years BP (Figure 3A; Neves and Piló, 2003; Auler et al., 2006; Ribeiro et al., 2013, 2021; Dantas et al., 2013, 2017; França et al., 2014; Scherer et al., 2017; Pansani et al., 2019; Faria et al., 2020a), thus ranging from the Bonaerian to early Platan. This temporal distribution is very similar to that of the Pampean region and extends of 450,000 to 6,000 years BP (Figure 3B; Collantes et al., 1993; Suárez, 2003; Cione and Tonni, 2005; Politis et al., 2004; Messineo and Politis, 2009; Jonhson et al., 2012; Hubbe et al., 2012; Rafuse, 2013; Prado et al., 2015). Our data indicate the presence of megafauna in South America until 3,500 years RC BP, which corresponds to the late Platan (Figure 3C).

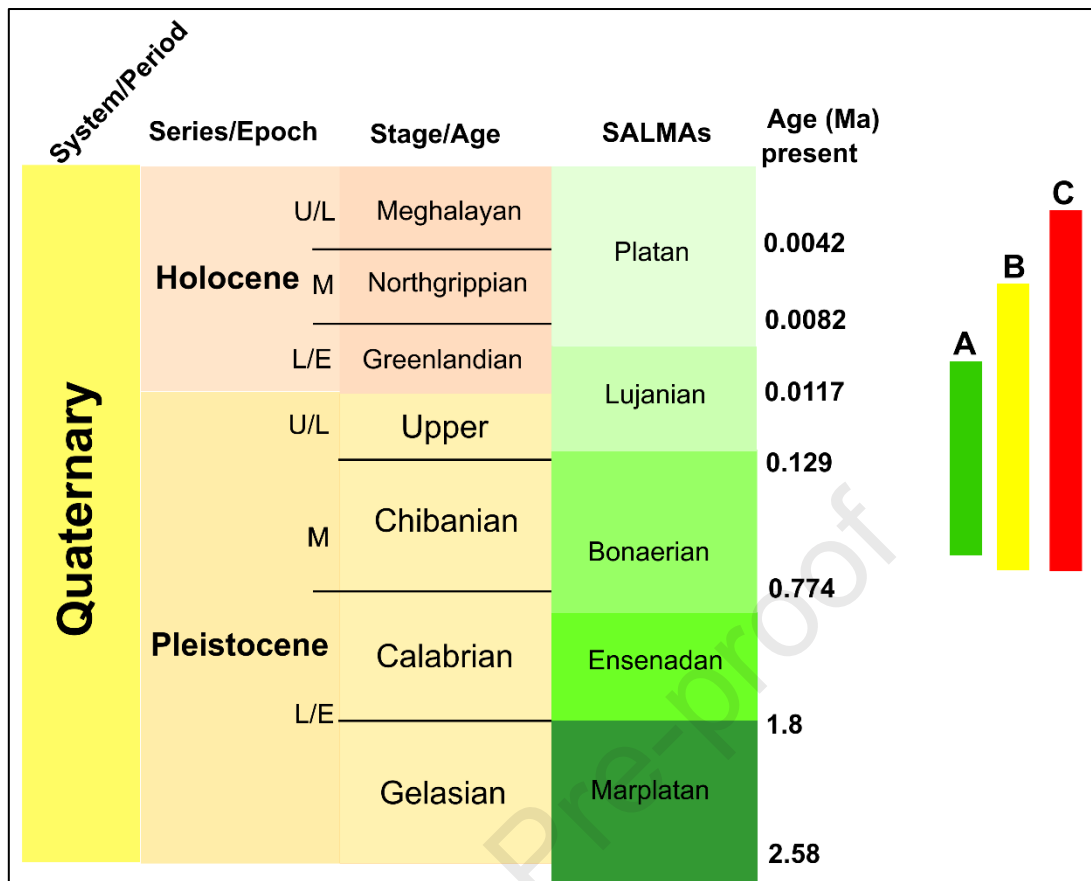


Figure 3: Quaternary time scale with the South American Land Mammal Ages (SALMAs); A - Temporal distribution of megafauna in BIR, as inferred solely from previously published data; B - temporal distribution of megafauna in South America; C - temporal distribution of megafauna in BIR, incorporating both previously published data and data from the present work.

Table 2: Holocene geochronological data from different locality in the Americas, obtained through different dating methods. The acronyms represent Brazilian states of CE (Ceará State); MS (Mato Grosso do Sul State); MG (Minas Gerais State); BA (Bahia State); SE (Sergipe State); AL (Alagoas State).

Taxon	Locality	Date (RC years BP)	Calibrated age (cal. BP)	Author/Method
<i>Eremotherium laurillardi</i>	Jirau – CE	6,161 ± 364	6,208 – 7,714	Present study
<i>Eremotherium laurillardi</i>	Jirau – CE	7,415 ± 167	7,867 – 8,536	Present study
<i>Smilodon populator</i>	Jirau – CE	7,803 ± 179	8,189 – 9,079	Present study
<i>Toxodontidae</i> indet.	Jirau – CE	7,804 ± 226	8,049 – 9,270	Present study
<i>Xenorhinotherium bahiense</i>	Jirau – CE	3,587 ± 112	3,493 – 4,217	Present study
<i>Notiomastodon platensis</i>	Jirau – CE	7,940 ± 502	7,836 – 10,159	Present study
<i>Palaeolama major</i>	Jirau – CE	3,492 ± 165	3,353 – 4,231	Present study
<i>Eremotherium laurillardi</i>	Miranda River – MS	5,942 ± 294	6,120 – 7,427	Present study
<i>Smilodon populator</i>	Lagoa Santa – MG	9,260 ± 150	10,260 – 10,480	Piló and Neves, 2003; AMS ¹⁴ C
<i>Catonyx cuvieri</i>	Lagoa Santa – MG	9,940 ± 40	11,320 – 11,600	Piló and Neves, 2003; AMS ¹⁴ C
<i>Toxodon platensis</i>	Toca dos Ossos – BA		10,664 – 10,790	Pansani et al., 20119; AMS ¹⁴ C
<i>Toxodon platensis</i>	Miranda River – MS		9,562 – 10,073	Pansani et al., 2019; AMS ¹⁴ C
<i>Eremotherium laurillardi</i>	Miranda River – MS		10,059 – 10,583	Pansani et al., 2019; AMS ¹⁴ C
<i>Toxodon platensis</i>	Baixa Grande – BA	9,000 ± 2,000		Ribiro et al., 2013; ESR
<i>Toxodontidae</i> indet.	João Dourado – BA	9,600 ± 1,000		Faria et al., 2020; ESR
<i>Toxodontidae</i> indet.	João Dourado – BA	9,100 ± 1,000		Faria et al., 2020; ESR
<i>Eremotherium laurillardi</i>	Poço Redondo – SE	9,720 ± 30	11,084 – 11,233	França et al., 2014; ¹⁴ C
<i>Eremotherium laurillardi</i>	Poço Redondo – SE	9,730 ± 30	11,089 – 11,273	França et al., 2014; ¹⁴ C

<i>Notiomastodon platensis</i>	Maravilha – AL	10,000 ± 500		Oliveira et al., 2010; ESR
<i>Notiomastodon platensis</i>	Poço Redondo – SE	10,044 ± 30		França et al., 2014; ¹⁴ C
<i>Eremotherium laurillardii</i>	Poço Redondo – SE	10,990 ± 30		França et al., 2014; ¹⁴ C
<i>Eremotherium laurillardii</i>	Poço Redondo – SE	11,010 ± 30		França et al., 2014; ¹⁴ C
<i>Cuvieronius humboldti</i>	Monte Verde – Chile	11,900 ± 200		Borrero, 1997; ¹⁴ C
<i>Scelidodon chiliensis</i>	Pampa de los Físiles - Peru	8,910 ± 200	9,780 – 10,150	Marshall et al., 1984; ¹⁴ C
Mylandontidae indet.	Santa Cruz – Argentina	8,639 ± 450		Borrero, 1997; ¹⁴ C
<i>Equus neogeus</i>	Arroyo Seco – Argentina	8,890 ± 90	9,740 – 10,150	Borrero et al., 1998; AMS
Mylandontidae indet.	Tucumã - Argentina	8,600 ± 150		Collantes et al., 1993; ¹⁴ C
<i>Megatherium americanum</i>	Arroyo Seco 2 – Argentina	8,390 ± 240		Borrero et al., 1998; AMS ¹⁴ C
<i>Megatherium americanum</i>	Arroyo Seco 2 – Argentina	7,320 ± 50		Borrero et al., 1998; AMS ¹⁴ C
<i>Hippidion saldiasi</i>	Pali Aike – Argentina	8,639 ± 450		Bird, 1988; ¹⁴ C
<i>Doedicurus clavicaudatus</i>	La Moderna – Argentina	7,510 ± 370		Politis et al., 2004; AMS ¹⁴ C
<i>Doedicurus clavicaudatus</i>	La Moderna - Argentina	7,460 ± 80		Politis et al., 2004; AMS ¹⁴ C
<i>Doedicurus clavicaudatus</i>	La Moderna – Argentina	7,010 ± 100		Politis and Gutierrez, 1998; AMS ¹⁴ C
<i>Doedicurus clavicaudatus</i>	La Moderna – Argentina	6,555 ± 160		Politis and Gutierrez, 1998; AMS ¹⁴ C
<i>Megatherium americanum</i>	Arroyo Seco 2 – Argentina	10,500 ± 90		Politis et al., 1995; AMS ¹⁴ C
<i>Equus neogeus</i>	Arroyo Seco 2 – Argentina	11,000 ± 100		Politis et al., 1995; AMS ¹⁴ C
<i>Equus neogeus</i>	Arroyo Seco 2 – Argentina	8,890 ± 90		Politis et al., 1995; AMS ¹⁴ C
<i>Equus sp.</i>	Arroyo Seco 2 – Argentina	8,390 ± 240		Politis et al., 1995; AMS ¹⁴ C
<i>Eutatus seguii</i>	Arroyo Seco 2 – Argentina	7,388 ± 74		Prado et al., 2015; ¹⁴ C
<i>Megatherium americanum</i>	Passo Otero – Argentina	9,560 ± 50		Jonhson et al., 2012; AMS ¹⁴ C
<i>Palaeolama sp.</i>	Arroyo Seco 2 – Argentina	9,775 ± 45		Prado et al., 2015; AMS ¹⁴ C
<i>Magalocnus rodens</i>	Cueva Beruvides – Cuba	6,250 ± 50		MacPhee et al., 1999; AMS ¹⁴ C
<i>Parocnus brownii</i>	Las Breas de San Felipe – Cuba	4,960 ± 280	4,950 – 6,350	MacPhee et al., 1999; AMS ¹⁴ C
<i>Parocnus brownii</i>	Las Breas de San Felipe – Cuba	10,250 ± 440	11,050 – 13,450	MacPhee et al., 1999; AMS ¹⁴ C
<i>Parocnus brownii</i>	Las Breas de San Felipe – Cuba	11,880 ± 420		MacPhee et al., 1999; AMS ¹⁴ C
<i>Parocnus brownii</i>	San Felipe – Cuba	4,690 ± 280		Iturralde-Vinent et al., 2000; AMS ¹⁴ C
<i>Neocnus come</i>	Trouing Ismays – Haiti	4,391 ± 42		Steadman et al., 2005; AMS ¹⁴ C

	Trouing Deron 1 –		
<i>Neocnus come</i>	Haiti	4,486 ± 39	Steadman et al., 2005; AMS ¹⁴ C
<i>Neocnus come</i>	Trouing Attie – Haiti	6,161 ± 45	Steadman et al., 2005; AMS ¹⁴ C
	Trouing Jeremy 5 –		
<i>Neocnus come</i>	Haiti	6,875 ± 47	Steadman et al., 2005; AMS ¹⁴ C
	Trouing Jeremy 5 –		
<i>Neocnus come</i>	Haiti	7,411 ± 51	Steadman et al., 2005; AMS ¹⁴ C
	Trouing Jeremy 5 –		
<i>Neocnus come</i>	Haiti	8,326 ± 57	Steadman et al., 2005; AMS ¹⁴ C
	Trouing Marassa –		
<i>Neocnus dousman</i>	Haiti	9,897 ± 65	Steadman et al., 2005; AMS ¹⁴ C
	St' Paul Island –		
<i>Mammuthus primigenius</i>	Alaska	7,908 ± 100	Guthrie, 2004; AMS ¹⁴ C
	Rampart, Arizona –		
<i>Nothrotheriops shastenses</i>	USA	11,000 ± 140	Long et al., 1974; AMS
	Rampart, Arizona –		
<i>Nothrotheriops shastenses</i>	USA	10,780 ± 200	Long et al., 1974; AMS
	Rampart, Arizona –		
<i>Nothrotheriops shastenses</i>	USA	11,020 ± 200	Long et al., 1974; AMS
	Rampart, Arizona –		
<i>Nothrotheriops shastenses</i>	USA	10,400 ± 275	Long et al., 1974; AMS
	Rampart, Arizona –		
<i>Nothrotheriops shastenses</i>	USA	10,035 ± 250	Long et al., 1974; AMS
	Rampart, Arizona –		
<i>Nothrotheriops shastenses</i>	USA	11,370 ± 300	Long et al., 1974; AMS
	Rampart, Arizona –		
<i>Nothrotheriops shastenses</i>	USA	11,480 ± 200	Long et al., 1974; AMS
	Muav Caves, Arizona		
<i>Nothrotheriops shastenses</i>	– USA	11,140 ± 160	Martin and Klein, 1984; AMS
	Muav Caves, Arizona		
<i>Nothrotheriops shastenses</i>	– USA	11,290 ± 170	Martin and Klein, 1984; AMS
	Shelter Cave, New		
<i>Nothrotheriops shastenses</i>	Mexico – USA	11,330 ± 370	Thompson et al., 1980; AMS

Table 2 presents geochronological data on megafauna from different locations in the Americas, demonstrating the survival of this mammalian fauna until the beginning of the late Holocene. This indicates that the extinction of megafauna did not occur in the Pleistocene-Holocene, as already indicated by Faure et al. (1999) and Vivo and Carmignotto (2004). The data in Table 2 demonstrate that the ages obtained in this analysis are the youngest obtained for BIR, with the age obtained for *Eremotherium laurillardi* (5,948 ± 294 RC years BP) in the Miranda River valley being the youngest age obtained for this taxon in South America. The ages obtained for *Xenorhintherium bahiense* (3,587 ± 112 RC years BP) and *Palaeolama major* (3,492 ± 165 RC years BP) from Itapipoca are the youngest obtained for the Americas. In Itapipoca, the dating of the taxa *P. major* and *X. bahiense* were isolated from the other taxa, for an interval of approximately 2,500 years BP. We interpret this temporal distance as that these species were actually the last representatives of megafauna to frequent this region, long after the extinction of the other species.

4.3 Hypothesis of BIR as a refuge for megafauna

The ages obtained in this analysis (Table 1) led us to postulate the hypothesis that the BIR had some areas functioning as environmental refuges during the early, middle and early

Holocene of the late Holocene. As demonstrated in the literature, all extinct megafauna taxa are associated with open environments (MacFadden and Shockey, 1997; Cartelle, 1999; Higgins and MacFadden, 2004), such as: savanna, woodland, grassland and steppe. Therefore, the survival of megafauna is related to the presence of open vegetation formations within the Caatinga and Cerrado biomes in the BIR, since plant species from these biomes were identified in the pollen record of Northeastern Brazil, from the last 40,000 BP years (Behling et al., 2000).

Itapipoca and Miranda are currently located in the Caatinga and "Cerradão", respectively, known generically as Seasonally Dry Tropical Forests (STDFs; Figure 4), through paleodistribution maps, according to Werneck et al. (2011). STDFs are characterized by the seasonality of the climate regime, with several months of intense drought characterized by a vegetational mosaic (Mooney et al., 1995): forests (deciduous and semi-deciduous), shrubs, cactus, woodland and grassland. "Cerradão" are deciduous and semi-deciduous forests, within the cerrado biome (savannah), being generically classified as STDFs (Werneck et al., 2011). These vegetation formations present a degree of particularities that differentiate them (xeromorphism and rainfall), with the Caatinga presenting hyper-xerophytic vegetation in arid locations.

Werneck et al. (2011) identified areas of STDF stability in South America, from the Last Glacial Maximum (LGM – late Pleistocene) to the mid-Holocene, in Northeast Brazil and also in the state of Mato Grosso do Sul (Figure 4). STDFs underwent fragmentation during the anomalous periods of humidity of the LGM in Northeast Brazil, detected through pollen records, at 40,000 years BP, 33,000 years BP, 24,000 years BP and between 15,500 and 11,800 years BP (De Oliveira et al., 1999; Behling et al., 2000). These periods were identified as the wettest for the region, with the expansion of Atlantic and Amazonian forests over areas of Caatinga (Behling et al., 2000; Furley and Metcalfe, 2007). These conditions possibly favored the isolation of megafauna populations in Northeast Brazil during the late Pleistocene, due to the expansion of forests.

From 10,540 years BP to 6,790 years BP, a gradual increase in aridity was observed in the Northeast region of Brazil (Cruz et al., 2009), generating conditions for the expansion of open environments and, consequently, greater availability of habitats for megafauna. This expansion of open environments was observed through pollen records, with the expansion of cerrado (savanna) over areas of arboreal caatinga in Northeast Brazil (De Oliveira et al., 1999). An increase in temperature and humidity is detected with the Holocene Climatic Optimum (HCO), with the establishment of modern caatinga vegetation in 4,535 years BP, with a predominance of tree and shrub species with low proportions of grasses and herbaceous (De Oliveira et al., 1999). HCO was a global event, between 6,500 and 4,000 years BP marked by high levels of humidity in relation to the LGM, causing the replacement of vast areas of open vegetation formations in forests or closed vegetation landscapes in tropical regions (30° latitude belt; Figura 4) from South America (Vivo and Carmignotto, 2004).

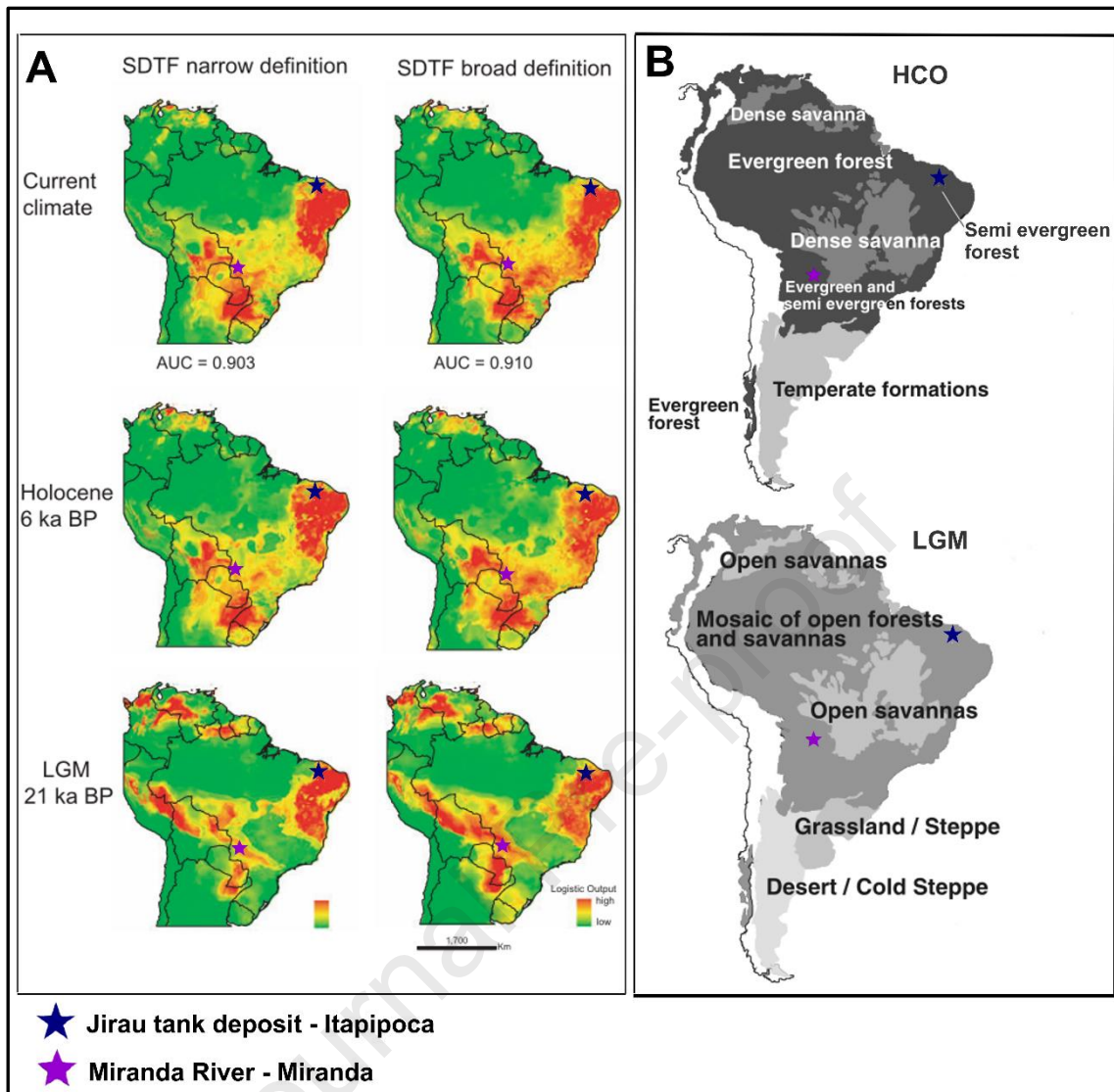


Figure 4: Paleodistribution maps of the main vegetation formations of South America. A – STDFs on narrow and broad definition for the LGM, middle Holocene and present (Werneck et al., 2011), the warmer colors correspond to regions with STDFs in South America; B – map of vegetation distribution during the HCO and LGM in South America (modified from Vivo and Carmignotto, 2004).

This described scenario indicates the expansion of closed environments with a drastic reduction in open environments, generating less favorable conditions for the survival of megafauna in the Northeast region of Brazil. The ages obtained in Itapipoca (Table 1) demonstrate the survival of megafauna species from the early Holocene to the beginning of the late Holocene. This, together with palynological and paleoclimatic data, demonstrate that after the Pleistocene/Holocene transition, the Northeast region presented environmental conditions favorable to the survival of megafauna until the beginning of the late Holocene. The environmental and climatic changes described above for the Brazilian Northeast indicate the presence of an environment favorable to the survival of mammalian megafauna in Itapipoca during the Holocene (Figura 4). Therefore, corroborating the hypothesis of Northeast Brazil as a refuge and, consequently, the Itapipoca region for megafauna until the beginning of the late Holocene.

Lagoa Negra (lake), located 200 km from the Miranda River Basin, has the only pollen record for the region (De Oliveira et al., 1999). Between 10,200 years BP and 8,770 years BP the pollen spectrum is dominated by aquatic plants (macrophytes) from shallow waters, grasses and herbaceous, indicating drier conditions than today and also large areas of grassland. From 8,870 years BP to 7,840 years BP the situation is reversed, with the pollen spectrum dominated by the presence of trees deciduous and semi-deciduous and gallery forest, while grasses are from aquatic environments. This indicates an expansion of forest environments over grassland, due to wetter conditions in the region. From 7,840 years BP, a reduction in tree and aquatic plant pollens was observed, indicating a reduction in precipitation, with an increase in grass and herbaceous, suggesting the expansion of grassland over forest areas. From 5,190 years BP to the present, a significant increase in arboreal and algal elements and small amounts of grass and herbaceous pollens was observed, indicating the expansion of forest areas with possibly small areas of grassland. The scenario described from palynological data obtained by De Oliveira et al. (1999), together with the age obtained for the Miranda River basin, indicates favorable conditions for the survival of megafauna until the middle Holocene (Figure 4).

The environmental changes described for both BIR locations indicate that these experienced diverse climatic and environmental conditions during the Holocene. The expansion and contraction of open environments, favorable to the survival of megafauna, during this period of time possibly generated the fragmentation and isolation of populations of megafauna species in the BIR. This cyclicity of fragmentation and expansion of open environments from the late Pleistocene to the beginning of the late Holocene may have generated favorable conditions for the extinction of megafauna, in which the locations of Itaipoca and the Miranda River valley may have sheltered the last populations of megafauna in South America.

4.4 Debating megafauna extinction theories

During the late Quaternary, the large and medium-sized mammal fauna of South America suffered the most significant extinction event among the continents, with around 80% of large mammals and 100% of megamammals being lost. To explain this important geobiological phenomenon, many hypotheses have been proposed, such as: climate changes during the Pleistocene/Holocene (Cartelle, 1999), overkill and blitzkrieg (Martin, 1984), expansion of forest environments during the HCO (Vivo and Carmignotto, 2004), asymmetry between continent and islands (Steadman et al., 2005), and “Broken Zig-Zag” (Cione et al., 2009).

Cartelle (1999) proposes that the extinction of megafauna in South America is associated with late Pleistocene climate change, due to the cold climate and dry conditions of the LGM. This theory does not explain how tropical vegetation types functioned in different climatic regimes and their consequences on large and megamammal fauna. Therefore, the different ages recorded from the early Holocene to the late Holocene, even if punctual in different locations in the Americas (Table 2), indicate that the extinction of megafauna did not occur in the Pleistocene-Holocene transition, but rather throughout the middle and late Holocene.

Another proposed theory is the asynchronous extinction of insular and continental megafauna, due to the ages obtained in Cuba and Saint Paul Island (Alaska; Table 2), being younger than the continental ages by thousands of years (Steadman et al., 2005). This hypothesis is supported by two lines of evidence: (1) radiocarbon ages of the last appearance of these animals that coincide with the arrival of humans in Cuba and Haiti; (2) if megafauna extinction were due to climate fluctuations, a concomitant extinction event between islands and

mainland would result. The data presented by Steadman et al. (2005) were incomplete, as their compilation of geochronological data excludes data from paleontological and archaeological sites with megafaunal skeletal remains of Early and Middle Holocene ages in Argentina (Table 2). The data presented in Table 2 corroborate argument 2, demonstrating that extinction on both islands and continents are associated with climatic and environmental changes, due to its synchronism with continental ages.

We do not consider the Overkill and Blitzkrieg theories (Mosimann and Martin, 1975; Whittington and Dyke, 1984) as the most plausible to explain the extinction of megafauna in South America, due to the long time of interaction between humans and megafauna, since the accepted age for the arrival of humans in the Americas is between 29,000 and 14,000 years BP (Guidon et al., 2000; Fariña and Castilha, 2007; Peyre et al., 2009; Lahaye et al., 2015; Dellehay et al., 2015; Boëda et al., 2016; Vialou et al., 2017). The ages presented in Table 2 and the arrival time of humans indicate a long time of interaction with megafauna, ruling out human activities as a driving force for the extinction of megafauna in South America.

The small number of studies addressing chronological data and interspecific relationships between humans and mammalian megafauna in the Americas as a whole does not corroborate the overkill and Blitzkrieg hypothesis. There are few archaeological sites with direct evidence of hunting of megafauna species in South America (Prous and Fogaça, 1999). In North America a similar situation was also observed, with only five species of megafauna known to be hunted by humans during the Clovis period (Grayson and Meltzer, 2003; Waters et al., 2014). This observation is also accepted by defenders of the Overkill hypothesis, such as Fiedel and Haynes (2004), due to the absence of strong archaeological evidence of interaction between megafauna and humans in the Americas. Archaeological evidence indicates that hunting was mainly focused on guanacos and deer, animals that survived the extinction (Cione et al., 2009). The scenario of preferential hunting by mega-mammals (Blitzkrieg) can be replaced by the modern view of hunting practices, where moderate and occasional hunting of the females, newborns and juveniles is necessary to generate extinction in thousands of years (Cione et al., 2009).

The autoecological factors may have contributed significantly to the extinction of South American megafauna, in a scenario of environmental stress due to environmental and climate changes during the late Pleistocene to the early late Holocene. The sexual maturity of almost all female mega-mammals is greater than ten years (Nowak, 1999). Pregnant females are more susceptible to hunters and predators, due to their reduced ability to perform evasive actions. The length of the lactation period is also another important factor to be considered, with a period exceeding 500 days being very common for large and mega-mammals (Hayssem and van Tienhoven, 1993). These autoecological factors over thousands of years in an environment of abrupt changes such as the late Quaternary, can have a negative impact on the number of megafauna individuals, generating increasingly smaller populations over time.

The theory of "Broken Zig-Zag", proposed by Cione et al. (2003), emphasizes that the extinction of the fauna of large and mega-mammals was caused by human hunters and gatherers. Favored by autoecological factors of the megafauna, abrupt environmental, climatic and distribution of open environments caused by the periodic oscillations that characterize the Late Quaternary, causing a considerable reduction of this fauna in response to cyclical environmental changes (Zig-Zag). The scarcity of archaeological records of interaction between humans and megafauna, as demonstrated above, does not support the theory that humans caused the extinction of megafauna. This leads us to believe that human activities played a supporting role in this event. Certainly, humans did not exterminate all large and mega-

mammals, but they did kill many of them, causing changes that caused their remnants to disappear (Kay, 2002).

Vivo and Carmignotto (2004) propose that the extinction of megafauna in South America is related to environmental changes that occurred during the mid-Holocene, more precisely during the HCO. The loss of megamammal lineages was attributed, by the authors, to the drastic reduction in the area of open vegetation (savannas, savanna woodland, grassland), directly affecting the availability of habitats and ecological niches that supported megafauna. This expansion of forest environments in South America during the HCO may have caused the population isolation of megafauna species and, consequently, a reduction in gene flow, generating conditions favorable to the extinction of megafauna. The ages obtained in this analysis (Table 1) corroborate the hypothesis raised by Vivo and Carmignotto (2004) of megafauna extinction during the middle Holocene. Therefore, the regions of Vale do Rio Miranda and Itapipoca during the HCO indicate the presence of environmental refuges for megafauna in these locations. Therefore, the theory proposed by Vivo and Carmignotto (2004) is the best options to explain the extinction process of large and megamammal fauna during the Holocene.

5. Conclusions

The ages obtained in this study are the most recent for the BIR. The ages of *Palaeolama major* ($3,492 \pm 161$ RC years BP) and *Xenorhinotherium bahiense* ($3,587 \pm 112$ RC years BP) are the youngest obtained so far for extinct megafauna in the Americas. The geochronological data obtained in this study and from other researchers demonstrate the presence of megafauna far beyond the Pleistocene/Holocene boundary, with a temporal distribution between 450,000 and 3,000 years BP in BIR. Geochronological, paleoclimatic and paleodistribution data of STDFs in South America corroborate the hypothesis that the Itapipoca and Miranda River valley locations were one of the last refuges of megafauna in South America. We believe that selective hunting of females and juveniles, autoecological factors of megafauna, are contributing attributes to the extinction of megafauna, with the driving force of this geobiological event being environmental/climatic changes during the LGM and the beginning of the late Holocene. It is likely that in the interglacials this fauna that was adapted to open environments did not die of starvation, but their populations may have been reduced under environmental stress. This caused isolation and reduced genetic flow between megafauna populations, due to the expansion of forest areas in South America, from the HCO to the present, creating conditions that promoted the extinction of the magnificent megafauna.

Acknowledgements

To FAPERJ (Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro) for funding the research (FAPERJ: E-26/202.047/2020; E-26/202.048/2020. E-26/200.828/2021; E-26/201.371/2021) and Conselho Nacional de Desenvolvimento Científico e Tecnológica (CNPq: 303596/2016-3; 305576/2021-6). We also thank the Museum of Prehistory of Itapipoca and the Zoology Laboratory of the Federal University of Mato Grosso do Sul, for having provided the fossils for carrying out the research.

References

- Ambrose, S. H., 1990. Preparation and Characterization of Bone and Tooth Collagen for Isotopic Analysis. *Journal of Archaeological Science*, 17, 431-451.
- Araújo-Júnior, H. I., Porpino, K.O., Ximenes, C. L., Bergqvist, L.P., 2013. Unveiling the taphonomy of elusive natural tank deposits: A study case in the Pleistocene of northeastern Brazil. *Paleogeography, Paleoclimatology, Paleoecology*, 378, 52-74.
- Araújo-Júnior H.I., Porpino K.O., Bergqvist L.P., 2017. Origin of bonebeds in Quaternary tanks deposits. *Journal of American Earth Sciences*. 76, 257– 63.
- Auler, A.S., Piló, L.B., Smart, P.L., Wang, X., Hoffmann, D., Richards, D.A., Edwards, R.L., Neves, W.A., Cheng, H., 2006. U-series dating and taphonomy of Quaternary vertebrates from Brazilian caves. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 240, 508 – 522.
- Barnosky, A.D., Lindsey, E.L., 2010. Timing of Quaternary megafauna extinction in South America in relation to human arrival and climate change. *Quaternary International*, 217(1-2), 10-29.
- Behling, H., Arz, H.W., Pätzold, J., Wefer, G., 2000. Late Quaternary vegetation and climate dynamics in northeastern Brazil, inferences from marine core GeoB 3104-1. *Quaternary Science Reviews*, 19, 981-994.
- Bocherens, H., Cotte, M., Bonini, R., Scian, D., Straccia, P., Soibelzon, L., Prevosti, F. J., 2016. Paleobiology of sabretooth cat *Smilodon populator* in the Pampean Region (Buenos Aires Province, Argentina) around the Last Glacial Maximum: Insights from carbon and nitrogen stable isotopes in bone collagen. *Paleogeography, Paleoclimatology, Paleoecology*, 449, 463-474.
- Boëda, E., Rocca, R., Da Costa, A., Fontugne, M., Hatté, C., Clemente-Conte, I., Santos, J., Lucas, L., Felice, G., Lourdeau, A., Villagran, X., Gluchy, M., Ramos, M.P.V., Lahaye, S., Guidon, N., Griggo, C., Pino, M., Pessis, A.M., Borges, C., Gato, B., 2016. New Data on a Pleistocene Archaeological Sequence in South America: Toca do Sítio do Meio, Piauí, Brazil. *PaleoAmerica*, 2(4), 286-302.
- Borrero, L.A., 1997. La extinción de la megafauna en la Patagonia. *Anales del Instituto de la Patagonia* 23: 89–102.
- Borrero, L.A., Zárate, M., Miotti, L., Massone, M., 1998. The Pleistocene-Holocene Transition and Human Occupations in the Southern Cone of South America. *Quaternary International*, 49/50, 191–199.
- Brock, F., Higham, T., Ditchfield, P., Ramsey, C.B., 2010. Current pretreatment methods for AMS radiocarbon dating at the Oxford Radiocarbon Accelerator Unit (ORAU). *Radiocarbon*, 52(1), 103-112.
- Cartelle, C., 1999. Pleistocene mammals of the Cerrado and Caatinga of Brazil. In: Eisenberg, J.B., Redford, K.H. (Eds.), *Mammals of the Neotropics. The Central Neotropics*. University of Chicago Press, Chicago, pp. 27-46.

- Cione AL, Tonni EP (1999) Biostratigraphy and chronological scale of uppermost Cenozoic in the pampean area, Argentina. In: Tonni EP, Cione AL (eds) Quaternary vertebrate palaeontology in South America. Quaternary South America Antartica Peninsula, 12:23–51.
- Cione, A.L., Tonni, E.P., (2005). Bioestratigrafía basada en mamíferos del Cenozoico superior de la región pampeana. In: Barrio R, Etcheverry RO, Caballé MF, Llambías E (eds) Geología y Recursos Minerales de la Provincia de Buenos Aires. Relatorio del XVI Congreso Geológico Argentino. La Plata 11:183–200.
- Cione, A.L., Tonni, E.P., Soibelzon, L.H., 2003. The broken zig-zag: Late Cenozoic large mammal and turtle extinction in South America. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"* 5:1–19.
- Cione, A.L., Tonni, E.P., Soibelzon, L.H., 2009. Did Humans Cause the Late Pleistocene-Early Holocene Mammalian Extinctions in South American in a Context of Shrinking Open Areas? In: American Megafaunal Extinctions at the End of the Pleistocene. Eds: Haynes, Springer Science.
- Collantes, M., Powell, J., Sayago, J.M., 1993. Formación Tafí del Valle (Cuaternario superior), provincia de Tucumán (Argentina): Litología, paleontología y paleoambientes. *Actas XII Congreso Argentino de Geología y II Congreso Exploración de Hidrocarburos* 1: 200–206.
- Cozzuol, M.A., Mothé, D., Avilla, L.S., 2012. A critical appraisal of the phylogenetic proposals for the South American Gomphotheridae (Proboscidea: Mammalia). *Quaternary International*, 255, 36-41.
- Cruz, F.W., Vuille, M., Burns, S.J., Wang, X., Cheng, H., Werner, M., Edwards, R.L., Karmann, I., Auler, A. S., Nguyen, H., 2009. Orbitally driven east-west antiphasing of South American precipitation. *Nature Geoscience*, 2, 210-214.
- Dantas, M.A.T., Cozzuol, M.A., 2016. The Brazilian Intertropical Fauna from 60 to about 10 Ka BP: Taxonomy, Dating, Diet and Paleoenvironments. In: Gasparini, G., Rabassa, J., Deschamps, C., Tonni, E., (eds) *Marine Isotope Stage 3 in South America, 60 Ka BP, 30 Ka BP*. Springer Earth System Sciences, Springer, 207-226p.
- Dantas, M.A.T., Dutra, R.P., Cherkinsky, A., Fortier, D.C., Kamino, L.H.Y., Cozzuol, M.A., Ribeiro, A.S., Vieira, F.S., 2013. Paleoecology and radiocarbon dating of the Pleistocene megafauna of the Brazilian intertropical region. *Quat. Res.* 79, 61 – 65.
- Dantas, M.A.T., Cherkinsky, A., Bocherens, H., Drefahl, M., Bernardes, C., França, L.M., 2017. Isotopic paleoecology of the Pleistocene megamammals from the Brazilian Intertropical Region: Feeding ecology ($\delta^{13}\text{C}$), niche breadth and overlap. *Quaternary Science Reviews*, 170, 152-163.
- DeNiro, M. J., 1985. Postmortem preservation and alteration of *in vivo* bone collagen isotope ratios in relation to paleodietary reconstruction. *Nature*, 317, 31.
- De Oliveira, P.E., Barreto, A.M.F., Suguio, K., 1999. Late Pleistocene/Holocene climatic and vegetational history of the Brazilian caatinga: the fossil dunes of the middle São Francisco River. *Paleogeography, Paleoclimatology, Paleoecology*, 152, 319-337.
- Dillehay, T.D., Ocampo, C., Saavedra, J., Sawakuchi, A.O., Mario Pino, R.M.V., Collins, M.B., Cummings, L.S., Arregui, I., Villagran, X.S., Hartmann, G.A., Mella, M., González, A., Dix, M., 2015. New archaeological evidence for an Early Human presence at Monte Verde, Chile. *PLOS ONE*, 10(12), 0145471.

- Dudley, J.P., 1996. Mammals, gompothores and the great American faunal interchange. In: Shoshani, J., Tassy, P., (Eds.), *The Proboscidea: Evolution and Paleoecology of Elephants and Their Relatives*. Oxford University Press, Oxford, pp. 289-295.
- Faria, F.H.C., Kinoshita, A., Pegorini, P., Carvalho, I.S., Araújo-Júnior, H.I., Figueiredo, A.M.G., Baffa, O., 2020a. ESR dating the late Quaternary megafauna fossil from João Dourado, Bahia, Brazil. *Journal South American Earth Science*, 101, 102586.
- Faria, F.H.C., Carvalho, I.S., Araújo-Júnior, H.I., 2020b. Genesis and taphonomic biases of Quaternary tank deposits of Northeastern Brazil. *Quaternary International*, 550, 184-193.
- Fariña, R.A., Castilla, R., 2007. Earliest evidence for human-megafauna interaction in the Americas. *Survey on Human and Faunal Relationships*, 31-34.
- Faure, M., Guérin, C., Parenti, F., 1999. The Holocene megafauna from the Toca do Serrote do Artur (São Raimundo Nonato archaeological area, Piauí, Brazil). *Comptes Rendus de l'Academie des Sciences, serie II fascicule A- Sciences de la Terre et des Planetes*, 329, 443-448.
- Ficarelli, G., Borselli, V., Herrera, G., Espinosa, M.M., Torre, D., 1995. Taxonomic remarks on the South American mastodons referred to *Haplomastodon* and *Cuvieronius*. *Geobios*, 28(6), 745-756.
- Ficarelli, G., Coltorti, M., Moreno-Espinosa, M., Pieruccini, P.L., Rook, L., Torre, D., 2003. A model for the Holocene extinction of the mammal megafauna in Ecuador. *Journal of South America Earth Science*, 15, 835-845.
- Fernicola, J.C., Porpino, K.O., 2012. Exoskeleton and Systematics: A historical problem in the classification of Glyptodons. *Journal of Mammalian Evolution*, 19, 171-183.
- Fiedel, S., Haynes, G., 2004. A premature burial: comments on Grayson and Meltzer's Requiem for Overkill. *Journal of Archaeological Science*, 31, 121-131.
- França, L.M., Dantas, M.A.T., Bocchiglieri, A., Cherkinsky, A., Ribeiro, A.S., Bocherens, H., 2014. Chronology and ancient feeding ecology of two upper Pleistocene megamammals from the Brazilian Intertropical Region. *Quat. Sci. Rev.* 99, 78 – 83.
- Furley, P.A., Metcalfe, S.E., 2007. Dynamic changes in savanna and seasonally dry vegetation through time. *Progress in Physical Geography*, 31, 633-642.
- Grayson, D.K., Meltzer, D.J., 2003. A requiem for North American overkill. *Journal of Archaeological Science*, 30, 585-593.
- Guidon, N., Peyre, E., Guérin, C., Coppens, Y., 2000. Resultdo da datação de dentes humanos da Toca do Garrincho, Piauí – Brasil. *Clio. Série Arqueológica, Recife*, 14, 75 – 86.
- Guthrie, R. D., 2004. Radiocarbon Evidence of mid-Holocene Mammoths Stranded on na Alaska Bering Sea Island. *Nature* 429, 746-748.
- Hayssen, V., van Tienhoven, A., 1993. Asdell's patterns of mammalian reproduction. A compendium of species-specific data. Comstock, Ithaca, NY.
- Higgins, P., MacFadden, B.J., 2004. "Amount Effect" recorded in oxigen isotopees of La Glacial horse (*Equus*) and bison (*Bison*) teeth from the Sonoran and Chihuahuan deserts, southwestern United States, *Paleogeography, Paleoclimatology, Paleoecology*, 206, 337-353.

- Hubbe, A., Hubbe, M., Neves, W., 2007. Early Holocene survival of megafauna in South America. *J. Biogeogr.* 34 (9), 1642-1646.
- Hubbe A., Hubbe M., Karmann I., Cruz F.W., Neves W.A., 2013. Insights into Holocene megafauna survival and extinction in southeastern Brazil from new AMS ^{14}C dates. *Quaternary Research*, 79:152–157.
- Iturralde-Vinent, M., MacPhee, R. D. E., Díaz-Franco, S., Rojas-Consuegra, R., Suárez, W., Lomba, A., 2000. Las Breas de San Felipe, a Quaternary Fossil Asphalt Infiltration near Martí (Matanzas Province, Cuba). *Caribbean Journal Science*, 36, 300–313.
- Johnson, E., Holliday, V.T., Martínez, G., Gutiérrez, M., Politis, G., 2012. Geochronology and landscape development along the middle Río Quequén Grande at the Paso Otero locality, Pampa Interserrana, Argentina. *Geoarchaeology* 27 (4), 300-323.
- Kay, C.E., 2002. False gods, ecological myths, and biological reality. In: Kay, C.E., Simmons, R.T., (eds) *Wilderness and political ecology*. University of Utah Press, Salt Lake City, pp 238–261.
- Lahaye, C., Guérin, G., Boëda, E., Fontugne, M.R., Hatté, C., Frouni, M., Clemente-Conte, I., Pino, M.A., Felice, G.D., Guidon, N., Lourdeau, A., Pagli, M., Pessis, A.M., Da Costa, A., 2015. New insight into a late Pleistocene human occupation in America: the Vale da Pedra Furada complete chronological study. *Quaternary Geochronology*, 30, 445-451.
- Lucas, S.G., 2009. Case 3480 *Mastodon waringi* (currently *Haplomastodon waringi*: Mammalia, Proboscidea): proposed conservation of usage by designation of a neotype. *Bulletin of Zoological Nomenclature* 66, 164-167.
- Long, A., Martin, P. S., Hansen, R. M. 1974. Extinction of the Shasta Ground Sloth. *Geol. Soc. Am. Bull.* 85, 1843–1848.
- Macario K.D., Alves, E.Q., Moreira, V.N., Oliveira, F., 2017. Fractionation in the graphitization reaction for ^{14}C -AMS analysis: The role of Zn x the role of TiH_2 . *International Journal of Mass Spectrometry*. 1(423):39-45.
- MacFadden, B.J., Shockey, B.J., 1997. Ancient feeding ecology and niche differentiation of Pleistocene mammalian herbivores from Tarija, Bolivia: morphological and isotopic evidence. *Paleobiology*, 23, 77–100.
- MacPhee, R.D.E., Flemming, C., Lunde, D.P., (1999). “Last” occurrence of the Antillean insectivore *Nesophontes*: new radiometric dates and their interpretation. *American Museum Novitates* 3264, 1–19.
- Marshall, L., Berta, A., Hoffstetter, R., Pascual, R., Reig, O.A., Bombin, M., Mones, A., 1984. Mammals and stratigraphy: geochronology of the continental mammal bearing Quaternary of South America. *Paleovertebrata Mem. Extr.*, 1-76.
- Martin, P. S., Klein, R. G., (1984). Eds., *Quaternary Extinctions: A Prehistoric Revolution* (Univ. of Arizona Press, Tucson).
- McNeish, R.S., Berger, R., Protscha, R., 1970. Megafauna and Man from Ayacucho, Highland Peru. *Science*, 168 (3934): 975-977.

- Messineo, P., Rivas, M., Soncini, J., 2002. Sitio Campo Laborde (Pdo. de Olavarría, Pcia. de Buenos Aires). Resúmenes del III Congreso de Arqueología de la Región Pampeana Argentina, Olavarría: 14-15
- Messineo, P., Politis, G.G., 2009. New radiocarbon dates from the Campo Laborde site (Pampean Region, Argentina) support the Holocene survival of giant ground sloth and glyptodonts. *Curr. Res. Pleist.* 26, 5-9.
- Mooney, H.A., Bullock, S.H. & Medina, E., 1995. Introduction. Seasonally dry tropical forests (ed. by S.H. Bullock, H.A. Mooney and E. Medina), pp. 1–8. Cambridge University Press, Cambridge.
- Mosimann, J. E., Martin, P.S., 1975. Simulating Overkill by Paleoindians. *American Science*. 63, 304.
- Mothé, D., Avilla, L.S., Cozzuol, M., Winck, G.R., 2012. Taxonomic revision of the Quaternary gomphotheres (Mammalia Proboscidea: Gomphotheriidae) from the South American lowlands. *Quaternary International*, 276-277, 2-7.
- Neves, W.A., Piló, L.B., 2003. Solving Lund's dilemma: new AMS dates confirm that humans and megafauna coexisted at Lagoa Santa. *Current Research in the Pleistocene* v.20, p.57–60.
- Nowak, R.M., 1999. Walker's Mammals of the world, 6th ed., vols I & II. Johns Hopkins University Press, Baltimore.
- Oliveira, F., Macaraio, K., Silva, K., Pereira, B.B., 2021. Preliminary radiocarbon dating results of bone samples at the LAC-UFF, Brazil. *Radiocarbon*, 63(4): 1103–1114, 2021b.
- Oliveira, E.V., Porpino, K.O., Barreto, A.F., 2010. On the presence of Glyptotherium in the Late Pleistocene of Northeastern Brazil, and the status of Glyptodon and Chlamydotherium. Paleobiogeographic implications. *Neues Jahrbuch für Geologie und Paleontologie. Abhandlungen*, 258, 353-363.
- Pansani, T.R., Oliveira, A.M., Pacheco, M.L.A.F., 2016. New occurrence of Pleistocene megafauna in Mato Grosso do Sul. *Revista do Instituto Geológico*. 37, 73-85.
- Pansani, T.R., Muniz, F.P., Cherkinsky, A., Pacheco, M.L.A.F., Dantas, M.A.T., 2019. Isotopic paleoecology ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$) of Late Quaternary from Mato Grosso do Sul and Bahia states. *Brazil* 221, 105864.
- Peyre, E., Guérin, C., Guidon, N., Coppins, Y., 1998. Des restes humains pléistocène dans la grotte du Garrincho, Piauí, Brésil. In: *Comptes rendus de l'Académie des Sciences, Sciences de la terre et des planetes*, 327: 335-360.
- Peyre, E., Granat, J., Guidon, N., 2009. Dentes e crânios humanos fósseis da Toca do Garrincho (Brasil) e o povoamento antigo das Américas. *Fundamentos*, São Raimundo Nonato, 8, 62-69.
- Piló, L.B., Neves, W.A., 2003. Novas datações ^{14}C (AMS) confirmam a tese da coexistência do homem com a megamastofauna pleistocênica da região cárstica de Lagoa Santa, MG. In: *XXVII Congresso Brasileiro de Espeleologia*.
- Politis, G., Prado, J.L., Beukens, R., 1995. The human impact in Pleistocene-Holocene extinctions in South America. The Pampean case. *Ancient Peoples and Landscapes* (E. Johnson, ed.), Lubbock, Texas: 187-205.

- Politis, G.G., Gutiérrez, M.A., 1998. Gliptodontes y cazadores-recolectores de la región pampeana (Argentina). *Lat. Am. Antiq.* 9 (2), 111–134.
- Politis, G.G., Messineo, P.G., Kaufmann, C.A., 2004. El poblamiento temprano de las llanuras pampeanas de Argentina y Uruguay. *Complutum* 15, 207-224.
- Politis, G.G., Messineo, P.G., Stafford Jr, T.W., Lindsey, E.L., 2019. Campo Laborde: A Late Pleistocene giant ground sloth kill and butchering site in the Pampas. *Science Advances*, 5, 1-10.
- Porpino, K.O., Fernicola, J.C., Bergqvist, L.P., 2009. A new cigulate (Mammalia: Xenarthra), *Pachyarmatherium brasiliense* sp. nov., from the Late Pleistocene of Northeastern Brazil. *Journal of Vertebrate Paleontology*, 29, 881-893.
- Porpino, K.O., Fernicola, J.C., Cruz, L.E., Bergqvist, L.P., 2014. The Intertropical Brazilian species (Xenarthra, Cingulata, Glyptodontoidea): a reappraisal of their taxonomy and phylogenetic affinities. *Journal of Vertebrate Paleontology*, 34, 1165-1179.
- Prado, J.L., Alberdi, M.T., Martínez, G., Gutiérrez, M.A., 2005. Equus (Amerhippus) neogeus LUND, 1840 (Equidae, Perissodactyla) at Paso Otero 5 site (Argentina): its implications for the extinction of the southamericanhorse. *N.Jb. Geol. Palaont.* 8, 449-468.
- Prado, J.L., Martinez-Maza, C., Alberdi, M.T., 2015. Megafauna extinction in South America: A new chronology for the Argentine Pampas. *Paleogeography, Paleoclimatology, Paleoecology*, 425: 41-49.
- Prous, A., Fogaça, E., 1999. Archaeology of the Pleistocene-Holocene boundary in Brazil. *Quaternary International*, 53/54, 21–41.
- Rafuse, D.J., 2013. Integridad del registro arqueofaunístico del sitio Arroyo Seco 2 (región Pampeana, Argentina) desde una perspectiva tafonómica. *FACSO-UNICEN, Olavarria*.
- Ribeiro, R.C., Kinoshita, A., Figueiredo, A.M.G., Carvalho, I. S., Baffa, O., 2013. Electron Spin Resonance Dating of the late Quaternary Megafauna Fossils from Baixa Grande, Bahia, Brazil. *Quaternary International*. 317: 91-96.
- Ribeiro, R.C., Kinoshita, A., Figueiredo, A.M.G., Carvalho, I. S., Araújo-Júnior, H.I., Baffa, O., 2021. ESR dating of Toxodon teeth from Baixa Grande, Bahia, Brazil. *Journal South American Earth Science*. 112: 103616.
- Schwarcz, H.P., Harmeet Nahal, 2021. Theoretical and observed C/N in human bone collagen. *Journal of Archaeological Science*, 131, 105396.
- Smits, E., Millard, A.R., Nowell, G., Pearson, D.G., 2010. Isotopic investigation of diet and residential mobility in the Neolithic of the lower Rhine basin. *Europe Journal Archaeological*, 13, 5-3.
- Suárez, R., 2003. Paleoindian components of northern Uruguay: New data on early human occupations of the Late Pleistocene and Early Holocene. In: Miotti L, Salemme M, Flegenheimer N (eds) *Where the south winds blow. Ancient evidence of Paleo South Americans*. Center for the Study of the First Americans, 29–36.
- Steadman, D.W., Martin, P.S., MacPhee, R.D.E., Jull, A.J.T., McDonald, H.G., Woods, C.A., Iturralde-Vinent, M., Hodgins, G.W.L., 2005. Asynchronous extinction of late Quaternary sloths on continents and islands. *PNAS* 102: 11763–11768.

- Scherer, C.S., Pales, L.F.M., Rosa, M., Silva, S.A., 2017. Chronological, taphonomical, and paleoenvironmental aspects of a Late Pleistocene mammalian fauna from Guanambi, Bahia, Brazil. *J. S. Am. Earth Sci.* 79, 95 – 110.
- Steele, J., Politis, G., 2009. AMS ^{14}C dating of early human occupation of southern South America. *J. Archaeol. Sci.* 36, 419-429.
- Steadman, D.W., Martin, P.S., MacPhee, R.D.E., Jull, A.J.T., McDonald, H.G., Woods, C.A., Iturralde-Vinent, M., Hodgins, G.W.L., 2005. Asynchronous extinction of late Quaternary sloths on continents and islands. *PNAS* 102: 11763–11768.
- Thompson, R. S., Van Devender, T. R., Martin, P. S., Foppe, T., Long, A., 1980. Shasta Ground Sloth (*Nothrotheriops shastense* Hoffstetter) at Shelter Cave, New Mexico: Environmentm diet, and extinction. *Quaternary Research*, 14, 360–376.
- Vialou, D., Benabdelhadi, M., Feathers, J., Fontugne, M., Vialou, A, V., 2017. Peopling South America's centre: the Late Pleistocene site of Santa Elina. *Antiquity*, Cambridge, 91(358): 865-884.
- Vivo, M., Carmignotto, A.P., 2004. Holocene vegetation changes and the faunas of South America and Africa. *Journal of Biogeography*, 31, 943–957.
- Waters, M., Thomas W. S. Jr., Kooyman, B., Hills L.V., (2014) Late Pleistocene horse and camel hunting at the southern margin of the ice-free corridor: Reassessing the age of Wally's Beach, Canada. *PNAS* 112:4263-4267.
- Werneck, F.P., Costa, G.C., Colli, G.R., Prado, D.E., Jack, W.S.Jr., 2011. Revisiting the historical distribution of Seasonally Dry Tropical Forest: new insights based on paleodistribution modelling and palynological evidence. *Global Ecology and Biogeography*, 20, 272-288.
- Whittington, S. L., Dyke, B., (1984). In: *Quaternary Extinctions: A Prehistoric Revolution*, P. S. Martin, R. G. Klein, Eds. (Univ. of Arizona Press, Tucson, AZ), pp. 451-465.

Highlights (3,500 years BP: The last survival of the mammal megafauna in the Americas) - Journal of South American Earth Science

- The article presents the youngest ages of South American mammal megafauna
- Two ages obtained are the youngest for the Americas
- Ages demonstrate survival of mammalian megafauna until the Late Holocene
- The Broken Zig-Zag theory is the best suited to explain megafauna extinction

Declaration of competing interest

The authors declare to the Journal of South American Earth Sciences that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.